Sibling aggression and mortality among nesting eagles

Article *in* Ibis · April 2008

DOI: 10.1111/j.1474-919X.1974.tb00243.x

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25 August 1973

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SIBLING AGGRESSION AND MORTALITY AMONG NESTLING EAGLES

Because many fights between eaglets have been observed, particularly in the eyries of Golden Eagles *Aquila chrysaetos* (e.g., Knight 1927, Gordon 1927: 34, Sumner 1934), the belief prevails that the second chick is killed by the first (Ingram 1959, Amadon 1964, Brown 1970: 81). Terms such as 'Cain and Abel battle', 'fratricide' or 'Cainism', have been used, although existing literature contains no record of observations from a hide of the entire sequence of events from hatching to the disappearance of the younger chick. In two such cases, I have been able to observe the whole process; other findings reported below were made in the course of attempts artificially to reduce nestling mortality by the transfer of eaglets to other eyries (Meyburg 1970, 1971, 1972, Meyburg & Garzón Heydt 1973).

Lesser Spotted Eagle *Aquila pomarina*

In this species two chicks usually hatch, but no more than one fledges. During transfer experiments in 1968, 1969 and 1970 in eastern Slovakia, it was observed that eaglets were extremely aggressive towards each other, in one case up to about two weeks before leaving the eyrie. From the age of one week, a chick placed on a table would crawl towards a smaller eaglet within a radius of 0.5 m, and attack—in one trial, ten times in rapid succession. The chicks attacked fled to the edges of the eyries where they died from cold or starvation, of fell out. In cases where the difference in size between the two siblings was small, and the second should have been able to secure a share of food (and did so during the first few days) this behaviour (which I term 'acceptance of intimidation') was evidently the indirect cause of death. As an example, on 15 June 1968 a chick was found dead on the ground beneath its eyrie. It had suffered no injury, nor had down been torn

from its back. This chick weighed 128 g (cf. an average weight of the second chick at hatching of 49 g, Meyburg 1970), and had evidently fed.

It is likely that, when the interval between the hatching of the two chicks is small, the older has no opportunity to intimidate the younger so long as the female broods continuously. Thus, in another eyrie, on 14 June 1968, both chicks were lively, weighing respectively 165 and 110 g.

In five experimental trials, when two chicks of identical size were placed together in an eyrie, one was invariably intimidated by the other. This response was usually observed within a few minutes, in 12 h at most. This 'acceptance of intimidation' may be regarded as a mechanism which ensures that in no circumstances can two chicks leave the eyrie. In 1971 the entire sequence of events was observed from hatching to the disappearance of the second chick, which in this eyrie was considerably smaller and weaker than the first:

At 16.00 hrs on 15 June this eyrie contained one chick (weight 138 g) and an egg in the course of hatching (72 g). At about 10.25 on 16 June the second chick finally hatched (49 g) and was immediately attacked by the first (now 148 g). During the period 16.12–16.21 hrs the mother fed 36 pieces of flesh, and during 19.05–19.25 hrs 56 pieces, to the first chick. The second did not attempt to feed, but lay, quite limp, in the nest bottom. When first observed at 07.00 on 17 June, the first chick already had a full crop, and the second was nowhere to be seen. During feeding periods from 10.55–11.06, 12.45–12.57 and 14.28–14.32 hrs, the female fed 21, 36 and 5 pieces of flesh to the larger chick. At 14.34 she swallowed the remains of a rabbit and then seized the second chick—now seen to be dead—with her beak, as if an item of prey, but then laid it down again, and brooded. On 18 June I kept watch from 04.53 to 19.15. After the female had eaten twice, at 11.36 she seized the dead chick, and, within eight minutes, fed some of it to the first chick and ate the rest herself.

Although the dead second chick has been presumed to be eaten on some occasions, this is apparently the first direct observation of the process in an eagle (Brown 1970: 81).

Verreaux's Eagle *Aquila verreauxi*

This eagle is another in which the second chick always dies. Observations were made in 1971 at an eyrie in the Transvaal, South Africa:

On the evening of 28 July the eyrie contained two eggs, measuring 675 × 550 mm (99 g) and 647 × 538 mm (92 g). The larger egg—invariably the first to hatch according to Gargett (1971)—was in the process of hatching with a hole 1·6 mm in diameter, and the smaller had a minute crack. On 29 July at 09.00 hrs the first chick—which had meanwhile hatched completely—weighed 78 g, and had evidently not yet been fed. On 30 July at 08.00 the chick weighed 83 g and the hole in the second egg was larger. On the morning of 31 July the second chick had also hatched. On this day, both appeared to be very weak and made little movement. By the evening the first chick was dead and the second in such poor condition that I saw no chance of rearing it, even by intensive care. On the following morning, however, it was in a better state, and by 6 August it weighed 159 g. Unfortunately, it was later stolen from the eyrie.

One could suppose that the second egg in eagles like *A. pomarina* and *A. verreauxi* acts as a kind of 'reserve', ensuring that at least one eaglet will hatch and that one will fledge with certainty.

African Hawk-eagle *Hieraaetus fasciatus spilogaster*

Observations were made in the Transvaal, South Africa, in 1971:

On 1 August two eggs were present, measuring 75·2 × 53·4 mm (90 g) and 62·9 × 51·9 mm (82 g). The first chick hatched from the larger egg, probably on 4 August. In the afternoon of 9 August the second chick finally emerged. At 17.00, with an empty crop, it weighed 64 g while the first chick, with a full crop, weighed 111 g (Plate 4a). The larger chick was sitting in the eyrie half covering the smaller; similar observations in *Aquila pomarina* led Wendland (1958) to assume that the smaller chick is crushed by the larger. On 10 August, while the eyrie was under observation between 10.00 and 17.00 hrs, there were two feeding periods, from 14.32 to 14.50 and from 16.07 to 16.22 hrs. During the first, the smaller chick sat in the hollow of the eyrie, closer to the parent than the first chick (which was nearer the edge of the eyrie). Nevertheless, of a total of 53 pieces of flesh proffered, the parent held only one in front of the smaller chick first; when this chick failed to take it properly, the meat was given to the other. During the second feeding period, 4 out of 44 pieces were offered to the smaller chick; one of these was too big to be swallowed, and the three other pieces were eaten by

the female after being held briefly in front of the smaller chick, which was unable to take them quickly enough. The chicks were brooded during 31% of the observation period. Whenever they were uncovered, the older chick periodically pecked at its sibling.

On 11 August, under observation between 08.00 and 17.00, the smaller chick no longer made any effort to feed. The female once looked with interest as the larger chick pecked and tugged at his sibling. On 12 August at 16.40, the smaller chick was dead. By 10.00 on 13 August it had vanished. Although there was always a surplus of prey left in the eyrie, in its three days of life it had lost 28 g in weight and probably taken no food. During the same period the older chick gained 36 g (Fig. 1).

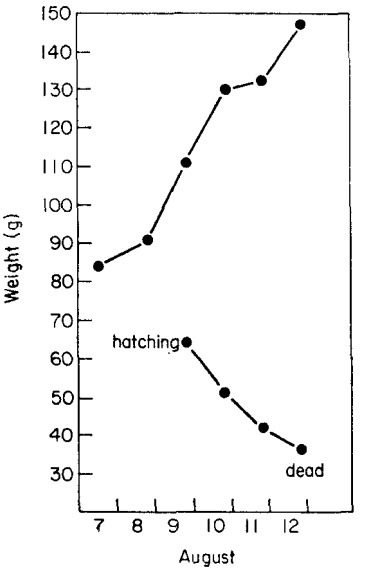

FIGURE 1. Successive weights of sibling African Hawk-eagle chicks from hatching to the death of the second chick.

Golden Eagle *Aquila chrysaetos*

Observations were made at an eyrie in the Lower Tatras, Czechoslovakia, in 1969:

On 8 May the two chicks weighed 530 and 355 g. The larger sat in the hollow of the eyrie and was warm, while the smaller, on the edge, was cold and emitting the typical 'cold cry'. All the down had been torn from a 9 cm square on its back, a clear indication of attacks by the elder sibling.

White-tailed Sea Eagle *Haliaeetus albicilla*

Fischer (1970: 60) contended that young White-tailed Sea Eagles, like young kites, are peaceable, but Moll (1970) described aggressive behaviour even between 5–6 week old siblings. My observations were made in an eyrie in the Danube Delta, Rumania, in 1969:

On 31 March, there were two chicks approximately one week old; weights could not be taken, but the difference in size was slight. Nonetheless, the larger chick pecked at the smaller, which remained motionless. When the female offered food and the smaller chick approached, the larger chick would seize the smaller by the nape of the neck and shake it, on release forcing it back to the extreme edge of the eyrie. Occasionally the older chick began to pluck the younger. Not until the larger had eaten his fill was the smaller sibling able to feed.

In the Tiergarten in Schönbrunn, Vienna, White-tailed Sea Eagles have bred many times. On the first two occasions on which it was established that two chicks hatched, one disappeared after a few days (Fiedler 1968). In 1969 the first egg was removed immediately after being laid, and returned when the second was laid; the two chicks thus hatched together and since both were reared (Fiedler 1970) this is an indication that shortage of food is not a determining factor in the death of the second chick.

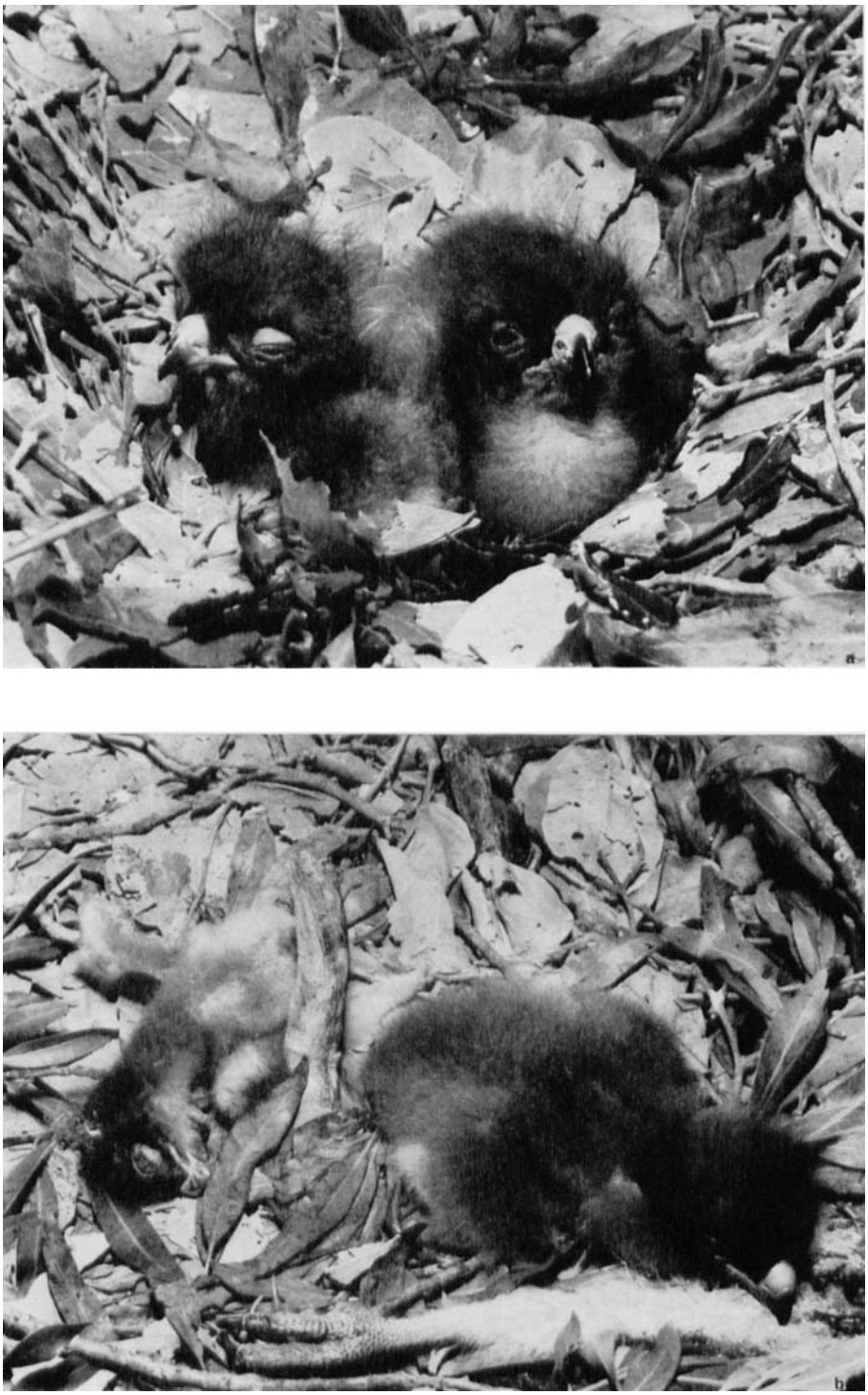

PLATE 4(a) The two chicks of the African Hawk-eagle on 9 August, the day the younger hatched. Only the older chick has a full crop and wide open eyes. (b) Three days later the second chick lies dead in the eyrie, from starvation.

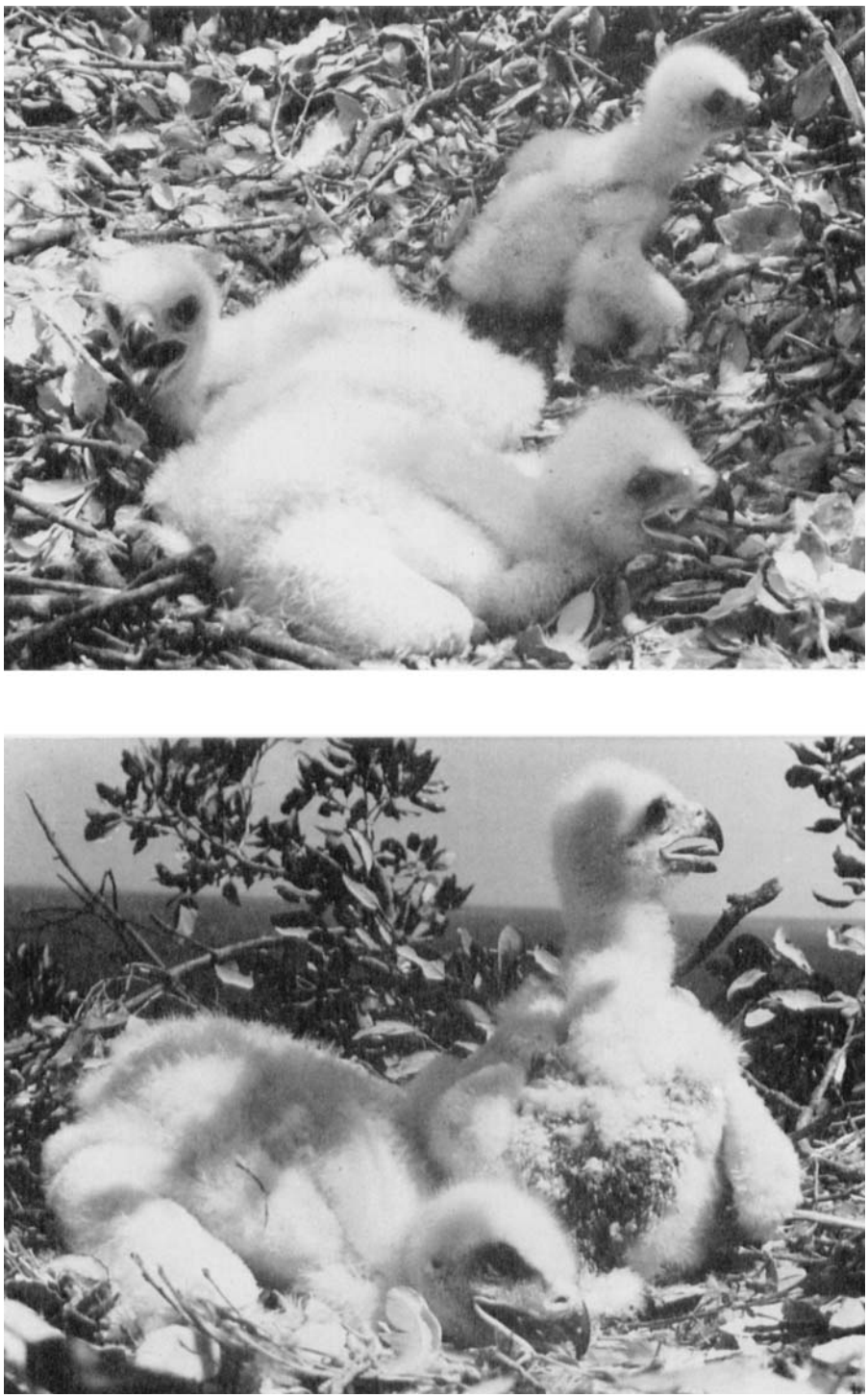

PLATE 5(a) Spanish Imperial Eagle eyrie on 24 April 1971 with three chicks, approximately 20 and 16 days old; two days later the smallest chick had disappeared without trace. (b) The same Spanish Imperial Eagle eyrie in 1972, on 27 April, with the first two chicks. Although one chick had been maltreated by its sibling, both later fledged.

Spanish Imperial Eagle *Aquila heliaca adalberti*

Observations were made in central western Spain, in 1971–73, at nests in which the broods varied from one to four nestlings (Meyburg 1974). In 1972, in two 3-egg clutches which hatched, the first hatchlings emerged simultaneously and the third four days later, indicating that incubation began after the lay of the second egg. In 1973, however incubation evidently began before the lay of the second egg: in three nests in which 3 eggs hatched, and one in which 4 eggs hatched, the first two chicks in each case hatched asynchronously. The loss of the smallest chick was observed in broods of two and three nestlings.

On 24 April 1971 an eyrie contained three downy chicks 16–20 days old, weighing 820, 780 and 340 g (Plate 5a). No prey remains were present. Two days later, the smallest chick had disappeared without trace. In the eyrie of the same pair the following year three chicks again hatched. The third was removed at hatching on 9 April 1972. On 27 April the lighter of the remaining two chicks (846 g) had the down torn from most of its back by its sibling (1006 g), leaving a large open wound. It did not however die, nor did it flee to the edge of the eyrie (Plate 5b).

On 29 April 1973 chicks from a 2-egg clutch weighed 316 g and 241 g; the smaller showed no signs of maltreatment, but still did not survive to fledge.

CONCLUSIONS

These observations suggest that the availability of food does not affect the chances of survival of the second chick in those species in which it never, or very rarely survives. The critical factor appears to be the interval between hatching, which is clearly variable. If, at the hatch of the second chick, the first is already skilful at taking pieces of flesh offered by the parent, then the younger sibling exerts little influence on the behaviour of the adult. At feeding times, it is offered fewer pieces of food and these, moreover, are proffered only briefly and in an inadequate fashion. The second chick soon dies of starvation. Attacks on it by its sibling are, by comparison unimportant.

If, on the other hand, the interval between hatching is short, then the second chick can develop normally so long as it is protected from its sibling's attacks by the brooding female parent. As soon as brooding is interrupted, the younger chick is subjected to the attack of the older. It is intimidated, no longer participates in feeding and flees to the edge of the eyrie. This process of the acceptance of intimidation, observed in the Lesser Spotted Eagle, quickly leads to the elimination of one chick, even when two of equal size are experimentally placed together, and explains why two chicks cannot normally be reared. The actual killing of one chick by another must happen extremely rarely, if at all.

In Golden Eagles and White-tailed Sea Eagles the factors determining the fate of the second chicks, some of which die and some of which survive to fledge, can be established only through further observation. The interval between hatching again is likely to be more critical than the availability of food at the time of hatching.

Totally different factors lead to the death of the youngest chick(s) in the Spanish Imperial Eagle. The eggs hatch asynchronously and, consequently, the sizes of the nestlings are staggered. Food shortage leads to the elimination of the smallest eaglet. This conforms to the classic pattern of the value of asynchronous hatching, as interpreted by Lack (1966).

I should like to express my sincere thanks to J. Švehlik, J. Garzón Heydt, Dr J. Palásthy, P. Johnson and W. Tarboton for their valuable support in the field, without which this work could not have been accomplished.

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CONTROLLED ANTIPHONAL CALLING BY WHOOPER SWANS

Paired Whooper Swans *Cygnus cygnus* are known to call together in a duet (Thorpe 1972). Johnsgard (1965) noted that initially the calling is alternate but ultimately becomes synchronous; he also indicated that the pen may have the slightly higher-pitched call. Armstrong (1947, 1963) gave a fine description of the calling ceremony, together with a discussion of its functions, but suggested that the pen calls a semitone lower than the cob. Scott (1950) not referring specifically to the pair calling ceremony, placed the cob's call five tones higher than the pen's. Thus far there has been no suggestion that the species is capable of maintaining a precisely timed antiphonal duet series, and examination of published recordings has failed to reveal any evidence. But a tape recording of Whooper Swans made by Patrick Sellar in southern Iceland in May 1967 shows controlled antiphonal calling with gradual and matched increase in duration of the constituent calls (Fig. 1).

The recording begins with the sound of slow wing-beats (3 p/s) against which can be heard three calls, each a little over 0·1 s, from the lower-pitched voice, henceforth referred to as bird 'A'. Between these calls are pauses of about 1·3 s; the third call is answered by bird 'B' with a call of similar duration but pitched a whole tone higher. The answering call by B appears to stimulate A to regular calling at 0·15 s intervals, with B answering the seventh call and overlapping the ninth and tenth (Fig. 3). At A's eleventh call, regular antiphonal calling is established and continues for fifteen complete duets; the timing is given in Table 1.

Apart from the regular alternation by A and B, the most interesting aspect of the series of duets is the graded increase in the duration of the calls, bird A beginning with a note of 0·09 s and ending with a note of 0·48 s while bird B, apparently taking its timing from A, begins with a 0·1 s note and ends with a 0·49 s note. Although the durational increase by